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Why productive upwelling areas are often sources rather than sinks of CO_2? – a comparative study on eddy upwellings in the South China Sea

N. Jiao[1,2], Y. Zhang[1,2], K. Zhou[1], Q. Li[1], M. Dai[1], J. Liu[1,2], J. Guo[1,2], and B. Huang[1]

[1]State Key Laboratory of Marine Environmental Sciences, Xiamen University, Xiamen 361005, China
[2]Institute of Marine Microbes and Ecospheres, Xiamen University, Xiamen 361005, China

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Correspondence to: N. Jiao (jiao@xmu.edu.cn)

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Abstract

Marine upwelling regions are known to be productive in carbon fixation and thus thought to be sinks of CO_2, whereas many upwelling areas in the ocean are actually sources rather than sinks of CO_2. To address this paradox, multiple biogeochemical parameters were investigated at two cyclonic-eddy-induced upwelling sites CE1 and CE2 in the western South China Sea. The results showed that upwelling can exert significant influences on biological activities in the euphotic zone and can either increase or decrease particulate organic carbon (POC) export flux depending on upwelling conditions such as the magnitude, timing, and duration of nutrient input and consequent microbial activities. At CE2 the increase of phytoplankton biomass caused by the upwelled nutrients resulted in increase of POC export flux compared to non-eddy reference sites, while at CE1 the microbial respiration of organic carbon stimulated by the upwelled nutrients significantly contributed to the attenuation of POC export flux, aggravating outgassing of CO_2. These results suggest that on top of upwelled dissolved inorganic carbon release, microbial activities stimulated by upwelled nutrients and phytoplankton labile organic carbon can play a critical role for a marine upwelling area to be a source rather than a sink of CO_2. Meanwhile, we point out that even though an upwelling region is outgassing, carbon sequestration still takes place through the POC-based biological pump as well as the refractory dissolved organic carbon (RDOC)-based microbial carbon pump.

1 Introduction

Upwelling is an oceanographic phenomenon that can bring nutrient-rich deep water upwards and thus can enhance phytoplankton carbon fixation in the euphotic zone (Mann and Lazier, 2006). Cyclonic eddies elevate isopycnals in the upper ocean and can form upwelling at different extents (Sweeney et al., 2003), and thus provide diverse scenarios for studies on subsequent biological responses. Some studies have

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reported eddy-induced upwelling areas to be sinks of CO_2 due to enhanced particulate organic carbon (POC) export flux (Beaulieu, 2002; Honjo et al., 1999; McGillicuddy et al., 1998, 2003; Newton et al., 1994; Siegel et al., 1999; Benitez-Nelson et al., 2007; O'Brien et al., 2013), while other studies suggest that eddies make a minor contribution to regional biogeochemical budgets (Oschlies and Garçon, 1998; Oschlies, 2002), and upwelling areas can be source rather than sinks of CO_2 (Rosón et al., 1999; Chen et al., 2007). Phytoplanktonic community structure shifts were reported to be of great importance in controlling POC-based biological pump (BP) carbon export from the surface ocean (Archer, 1995; Michaels and Silver, 1988; Boyd and Newton, 1999). When small-sized phytoplankton (e.g. *Prochlorococcus* and *Synechocccus*) dominates the community, the BP would not be distinct because picoplankton POC sinking rates are extremely low (Takahashi and Bienfang, 1983) unless they are aggregated (Richardson and Jackson, 2007), instead, they are effectively grazed by protozoa within the microbial loop (Azam et al., 1983; Glover et al., 1988). Eddy age is another interpretation of the extents of biological response and associated export flux since nutrient injection would subside as the eddy begins to decay (Sweeney et al., 2003). Despite these significant recognitions, one issue is still under wraps: While eddy-induced nutrient supply to surface waters increases primary production, elevated nutrients and consequently enhanced primary production could also stimulate microbial heterotrophic metabolisms that influence carbon respiration (Jiao et al., 2011) as well as carbon sequestration through the microbial carbon pump (MCP) (Jiao et al., 2010). Given that microbes are major contributors to both community respiration (CO_2 source) ($\sim$ 50 to $>$ 90 %; Rivkin and Legendre, 2001; Robinson and Williams, 2005) and refractory dissolved organic carbon (RDOC) (CO_2 sink) as the output of the MCP (Benner and Herndl, 2011), microbial activities remain the key aspect to be addressed in this regard. Based on the above understanding, we hypothesize that upwelling can either increase or decrease POC export flux depending on the environmental conditions and microbial activities, and thus can significantly influence the air-sea CO_2 exchanges. To test and verify this hypothesis, we conducted a comparative study with systematic biogeochemical obser-

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vations at two comparable cyclonic eddies in the South China Sea (SCS) at the same time. This paper aimed at linking microbial activities under different environmental conditions to the POC export through the BP, RDOC production by the MCP as well as CO_2 outgassing in upwelling areas toward a better understanding of the mechanisms and variability of the marine carbon sink.

2 Material and methods

2.1 Study sites

In the study area of the western SCS, two well-developed cold-core cyclonic eddies (CE1 and CE2) were identified and documented by Doppler Current Profiler (ADCP) data and negative sea-level anomaly during the GOE-2 cruise (on board RV Dongfanghong #2, 14 August to 14 September 2007) (Zhang et al., 2009, 2011a; Hu et al., 2011). The satellite altimetric history (http://argo.colorado.edu/~realtime/gsfc_global-real-time_ssh/) suggested intensification of CE1 (decaying) and CE2 (young) during our sampling. Biogeochemical surveys (Fig. 1) were carried out to localize the eddies. For particle flux analysis, thirty-seven sites were sampled. Biological measurements and incubations were conducted at four representative sites: TS1, Y12, Y56 and SEATS. TS1 and Y12 were located in the center of CE1 and CE2 respectively, and Y56 site at the CE1 boundary. SEATS site is the Southeast Asia Time-Series Study station, which is an outside-eddy site indicating background levels (Zhang et al., 2009) (Fig. 1).

2.2 Hydrographic parameters

A SeaBird CTD-General Oceanic rosette sampler with Go-Flo bottles (SBE 9/17 plus, SeaBird Inc., USA) was used to record temperature and salinity and to collect water samples. Samples for inorganic nutrients (nitrate + nitrite, phosphate, silicate) were filtered through 0.45 µm cellulose acetate filters and measured immediately onboard

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using a flow injection analyzer (Tri-223 autoanalyzer) and standard spectrophotometric methods (Su-Cheng et al., 1990). Oxygen concentrations were determined on board using the Winkler method (Carpenter, 1965). Apparent oxygen utilization (AOU) and oxygen saturation (O_2^S) were estimated based on in situ O_2, temperature and salinity (Garcia et al., 2006). The fluorescence of dissolved organic matter (FDOM) was measured on board using a Turner Designs (Model 10-AU, USA) fluorometer equipped with the FDOM optical kit at 310–390 nm excitation and at 400–600 nm emission after seawater was filtered through pre-cleaned 0.22 µm pore size polycarbonate membrane filters (Millipore). The fluorescence of the samples is expressed in quinine sulfate units (QSU) where 1 QSU is equivalent to the fluorescence of 1 µg L^{-1} quinine sulfate solution.

2.3 Phytoplankton analysis

Samples for photosynthetic pigments analysis were collected on 0.7 µm pore-size GF/F filters (Whatman). Photosynthetic pigments were extracted in N,N-dimethylformamide (Furuya et al., 1998) and analyzed using reverse phase HPLC on a C8 column and a modification of the method of Mantoura and Llewellyn (1983) and Van Heukelem et al. (2001), including peridinin, fucoxanthin, 19′-but-fucoxanthin, 19′-hex-fucoxanthin, neoxanthin, prasinoxanthin, violaxanthin, alloxanthin, lutein, zeaxanthin, chlorophyll *b*, divinyl-chlorophyll *a* and total chlorophyll *a*. Based on the pigment data, phytoplankton community composition was analyzed using CHEMTAX, including dinoflagellates, diatoms, haptophytes_4, haptophytes_3, chlorophytes, cryptophytes, *Prochlorococcus*, *Synechococcus* and prasinophytes (Mackey et al., 1996).

2.4 ^{234}Th analysis and particle flux estimation

High resolution sampling for total thorium-234 was conducted using recently developed small volume (2 or 4 L) MnO_2 co-precipitation method (Benitez-Nelson et al., 2001; Buesseler et al., 2001; Cai et al., 2006). Beta counting of ^{234}Th was carried

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out using a gas-flow proportional low-level beta counter (Model GM-25-5, RISØ National Laboratory, Denmark). Total ^{234}Th activity was calculated after recovery calibration and corrections from decay and ^{234}Th ingrowth from dissolved ^{238}U according to Cai et al. (2006). ^{238}U activity was calculated from the equation of

^{238}U (dpm L^{-1}) = 0.07081 × salinity (Chen et al., 1986). (1)

Export flux of ^{234}Th was determined through ^{234}Th/^{238}U disequilibria under the assumptions of steady state and no physical transport. Particle organic carbon (POC) export flux was determined according to the ratio of POC to ^{234}Th (Buesseler et al., 2006; Savoye et al., 2006), using the following equation:

POC flux = ^{234}Th flux × (POC/^{234}Th) (Buesseler et al., 2006). (2)

2.5 Heterotrophic microbial abundance, production and respiration estimates

Microbial abundance was determined by epifluorescence microscopy. Samples were stained with 4′,6′-diamidino-2-phenylindole (DAPI) and counted under a Zeiss Axioplan 2 epifluorescence microscope. To determine heterotrophic microbial production, water samples were incubated with [^{3}H]leucine (10 nM final concentration; 65 Ci mmol^{-1}, Amersham) at in situ temperature. The disintegrations per minute (DPM) were counted in a liquid scintillation counter and converted into leucine incorporation rates (Kirchman and Wheeler, 1998).

Microbial respiration rates were estimated indirectly. Since the term "bacterial respiration (BR)" is more commonly used in the literature, we used BR as microbial respiration here. Likewise terms "bacterial growth rate (BG)", "bacterial growth efficiency (BGE)" are used in correspondence.

BR = (BG × ICF × CCF) (1/BGE – 1) (Mourinõ-Carballido, 2009). (3)

BG is measured by the [^{3}H]-thymidine or [^{3}H]leucine technique; ICF and CCF are the isotope and carbon conversion factors; here, we used the ICF reported in Pacific

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by Kirchman (1992) (0.108×10^{18} cells mol^{-1} of incorporated leucine), the CCF of 20 fg C $cell^{-1}$ (Lee and Fuhrman, 1987) and the BGE reported for open ocean regions (0.08; Robinson, 2008).

2.6 pCO_2 determination and air–sea CO_2 flux estimation

Surface water xCO_2 (the mole fraction concentration of CO_2 in the dried sample gas flow) was measured using a LI-COR 7000 infrared gas analyzer coupled to a gas-water equilibrator according to Zhai et al. (2005). The water temperature right before the equilibration chamber was recorded with an YSI® temperature sensor. The partial pressure of CO_2 of the surface water at the temperature of equilibration [pCO_2 (eq), units: µatm], the partial pressure of CO_2 at the in-situ temperature [pCO_2 (water), units: µatm], the partial pressure of CO_2 in the air [pCO_2 (air), units: µatm] and the air–sea CO_2 flux on pixel i of a 0.1° longitude × 0.1° latitude grid were estimated according to Zhai et al. (2005). A positive value indicates a transfer of CO_2 from water to the atmosphere. Gas transfer velocity was calculated from wind speeds. Relationship of gas transfer velocity with wind speed proposed by Sweeney (2007) was used to provide the value of air–sea CO_2 flux.

3 Results and discussion

3.1 Upwelling nutrient supply to the euphotic zone and biological responses

The surface waters (upper 200 m) of both CE1 and CE2 exhibited lower temperature, higher salinity and higher nutrient levels as compared to the surrounding waters (Table 1; Fig. 2). Apparently, the cyclonic eddy isopycnal uplift resulted in shoaling of the nitracline at both cases (Fig. 2). Consequently the nutrients injected into the nutrient-depleted surface 50 m waters effectively stimulated phytoplankton growth as indicated by the increase of chlorophyll *a* concentration (Table 1, Fig. 3a). The total chlorophyll *a*

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maximum values at the eddy central sites of CE1 (TS1) and CE2 (Y12) were 0.65 and 0.75 μg L^{-1}, respectively, while only 0.46 and 0.35 μg L^{-1} at the CE1 periphery site Y56 and the reference site SEATS, respectively. Interestingly, while nitrogen and phosphorus were used up in the surface 50 m at both CE1 and CE2, silicate at CE1 seemed to be extra compared to CE2 (Fig. 2). Photosynthetic pigments analysis indicated that the dominant autotrophs at CE1 were cyanobacteria rather than diatoms as occurred at CE2 (Table 1, Fig. 3b and c), suggesting that diatoms in CE1 were surpassed by cyanobacteria and not well developed, allowing extra silicate left over in the environment. The less intense upwelling and consequently higher temperature (which favors cyanobacteria) at CE1 than CE2 could be responsible for the corresponding differences between their community structures. A clear pattern in the depth profiles of phytoplankton pigments was demonstrated: the maximum chlorophyll *a* depth (MCD) was the shallowest in the strongest upwelling area (CE2) where diatoms were dominant, but deeper in weak- or non-upwelling areas where *Prochlorococcus* were prevailing (Fig. 3a). As a result of biological interactions under upwelling impacts, heterotrophic microbes in the middle euphotic zone (50 m) got an abundance order among different sites (CE1 boundary > CE1 center > CE2 center) (Table 1) similar to *Prochlorococcus* (Fig. 3b), rather than to diatoms (Fig. 3c) (also see Sect. 3.3).

3.2 Responses of POC export flux

Total ^{234}Th activities varied with depth ranging from 0.42 ± 0.06 dpm L^{-1} at 2 m to 2.78 ± 0.08 dpm L^{-1} at 100 m in the whole study area. The mean values of ^{234}Th activities at 100 m of CE1, CE2 and surrounding non-eddy sites were 2.45, 2.41 and 2.32 dpm L^{-1}, respectively (Fig. 4). The largest disequilibrium between ^{234}Th and its parent ^{238}U occurred at the upper euphotic zone of CE2, indicating the highest particle export there. In contrast, the smallest export signals were observed in CE1 (Fig. 4). The POC fluxes at 100 m estimated through the ^{234}Th activity showed a similar pattern that the highest and lowest POC fluxes occurred in CE2 (6.16 ± 3.74 mmol C m^{-2} d^{-1}) and CE1 (2.50 ± 2.03 mmol C m^{-2} d^{-1}) respectively. Independent-samples *T* test ($p < 0.05$)

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analysis suggests that the difference in POC flux between CE1 and CE2 is significant (Table 1). Such difference is consistent to the difference in phytoplankton community structure that diatoms could contribute more POC export fluxes at CE2 than CE1.

3.3 Microbial respiration contributing to attenuation of POC export and CO_2 outgassing

In order to test whether microbial activity significantly influenced POC export flux in the two eddy-induced upwelling ecosystems, microbial abundance and activity were investigated at two representative stations of CE1, one station of CE2, as well as at St. SEATS (Fig. 1). Generally, microbial abundance decreased dramatically with depth, but showed distinct differences between the four sites. At 50 m where upwelling impacts were significant, the highest abundance was observed in CE1, while the lowest abundance occurred in the center of CE2 (Table 1). Leucine uptatke, as a measure of microbial activity, decreased with depth by two orders of magnitude within 200 m (Fig. 5). Like abundance, microbial activities at 50 m depth were also higher at the two stations in CE1 (17.08 and 18.62 pmol $L^{-1}h^{-1}$ at sites TS1 and Y56 respectively) than that in the center of CE2 (13.95 pmol $L^{-1}h^{-1}$ at site Y12). However, when abundance-specific (unicellular) leucine uptake rate is considered, the highest value was observed at the center of CE2 (Fig. 5). CE2 has been diagnosed to be more intense as the ADCP data documented counterclockwise currents of higher speed in CE2 (1.1 m s^{-1} at maximum) than in CE1 (0.7 m s^{-1}) (Zhang et al., 2011b), and the age of CE2 was younger than CE1 as seen from the satellite altimetric history. Thus, the microbial abundance in the shallow water of CE2 was likely diluted by the deep water with low microbial abundance, but the cell activity could be stimulated by labile organic carbon which was released from enhanced phytoplankton biomass. In CE1, POC export flux was the lowest whereas BR was the highest, corresponding to the highest air–sea CO_2 flux (4.15 ± 0.84 mmol m^{-2} d^{-1}) among all the investigation sites, which obviously can not be attributed to dissolved inorganic carbon (DIC) release as seen from the fact that CE2 rather than CE1 had the strongest upwelling and thus the strongest DIC release

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but the total CO_2 outgassing in CE2 is actually lower ($3.43 \pm 0.59\,mmol\,m^{-2}\,d^{-1}$) than CE1 ($4.15 \pm 0.84\,mmol\,m^{-2}\,d^{-1}$). That is, it was microbial activity who did matter for the upwelling area to be a source or sink of CO_2. As a matter of fact, in CE1, the average carbon loss by microbial respiration is about fifteen-fold the average POC export flux at 100 m (Table 1). The enhanced total microbial activity could have consumed more organic carbon leading to lower POC export flux and higher CO_2 outgassing in CE1 than the other sites (Table 1). The satellite altimetric and chlorophyll data series (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/batchDownload.cgi) suggested that the primary production at the initial stages of CE1 could be a little bit lower than that of CE2, but this difference was not enough to cause the large difference in POC export between CE1 and CE2. It is most likely that upwelling induced nutrient input enhanced phytoplankton biomass and labile organic carbon release which then stimulated bacterial growth and respiration. Then bacteria became more competent in attaching to and consumption of POC, consequently exacerbating the attenuation of the POC export flux. As for the case of CE2, a diatom-dominated community (Table 1) induced by nutrients supply would be the main reason for the high POC export flux. Taken together, the intensity and age of the two eddies and the different responses in phytoplankton community and microbial activity suggest that phytoplankton rapidly responded to upwelled nutrients, accumulating biomass and causing high POC export at the initial intensification period (such as the case of the of CE2); bacteria were subsequently stimulated by nutrients and labile DOC produced by phytoplankton resulting in high respiration rates during the later intensification period (such as the case of of CE1).

In literature, it is also reported in the northwestern subtropical Atlantic (Mouriño-Carballido, 2009) that centers of cyclonic eddies were associated with low net community production as the result of a noticeable increase in BR, although several observations have reported reduction in respiration rates in cyclonic eddies in the northeastern subtropical Atlantic (Gonzalez et al., 2001; Maixandeau et al., 2005) which could be attributed to lower microbial abundance or lower maintenance-respiration in heterotrophic microbes inside than outside the cyclonic eddy (Gonzalez et al., 2001).

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Although low BR could occur at certain upwelling stages as we observed in CE2 which was due to the low bacterial abundance diluted by deep water, enhancing of BR might be the prevailing feature of the cyclonic eddies (Table 2).

3.4 Microbial oxygen consumption and organic carbon transformation

AOU has been demonstrated as a useful indicator for microbial consumption of oxygen in the water column (Hayase and Shinozuka, 1995; Yamashita and Tanoue, 2008). In our study, both CE1 and CE2 had higher AOU values than the reference site (Table 1). The effects of oxygen consumption is also verified by the microbial metabolic output, the fluorescence of humic-type dissolved organic matter (FDOM), which was measured as an indicator of RDOC (Yamashita and Tanoue, 2008). Our earlier studies have showed that humic-type FDOM and the ratio of humic-like FDOM to bulk DOC concentrations was generally higher in the cyclonic eddy centers than the reference site St. SEATS, especially at 35 to75 m depths (Zhang et al., 2009). Here humic-type FDOM in the euphotic zone also displayed higher fluorescence intensity in the upwelling areas than the reference site. Furthermore, a significant positive correlation ($p < 0.01$) between AOU and FDOM was observed in the euphotic zone of CE1 where microbial respiration was strong (Fig. 6), suggesting that FDOM was associated with microbial decomposition of organic matter which consuming oxygen.

3.5 About CO_2 outgassing and carbon sequestration in upwelling areas

Our results suggest that when nutrient-rich deep water with low-abundance of microbes is upwelled to the upper euphotic zone, a corresponding bloom in phytoplankton such as diatoms and an initial reduction in total microbial respiration would result in increase of POC export flux, as demonstrated in the case of CE2. In the case that diatom blooms do not occur or picoplankton populations dominate the community, like the case of CE1, microbial loop develops and microbial respiration is mobilized, which exacerbates the

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attenuation of POC flux and could play a critical role for a marine upwelling area to be a source rather than a sink of CO_2.

Based on the above consideration, two scenario models are established (Fig. 7). When an upwelling bring nutrients to the upper layer of the euphotic zone where light is replete, diatoms respond and bloom enhancing POC export; meanwhile, total microbial respiration would be slowed down due to diluted abundance and low temperature by the deep water. As a result, export flux exceeds respiration flux (Fig. 7a; instance: CE2). If the upwelled nutrients can reach only the lower layer of the euphotic zone where picoplankton especially *Prochlorococcus* are dominant, diatoms do not respond much to the upwelling due to lack of enough light down there, instead, microbial loop could be very active (Hagström et al., 1988; Azam et al., 1993). As a result, microbial respiration flux would exceed POC export flux (Fig. 7b; instance: CE1).

In addition, a common sense that "outgassing areas are carbon sources" needs to be revised for the case of marine upwelling regions. As shown in Fig. 8, for a non-upwelling system, if $CO_{2\ in} < CO_{2\ out}$, it is a CO_2 source; whereas for a steady upwelling system, CO_2 released from DIC-rich deep water (DIC_{up}) has to be taken into consideration. Even if $CO_{2\ in} < (CO_{2\ res} + DIC_{up})$, it dose not mean no massive carbon sequestration in the system, and the sequestrated carbon dose not have to be all exported out as POC (POC_{exp}), it can be stored in the dissolved form as RDOC through the MCP approach (Jiao et al., 2010). Therefore, as long as it meets the condition $(CO_{2\ in} + DIC_{up} + POC_{exp} + RDOC) > CO_{2\ out}$, there is carbon sequestration, even if it is outgassing. Therefore, the adjudgement of a marine region to be a carbon sink or source should be carefully made on the long-term balance between the amount of outgassing carbon and the sum of the outputs of the BP and the MCP, rather than simply according to momentary CO_2 partial pressures.

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4 Summary

The results from the present study suggest that while upwelling usually enhances primary production through nutrients injection to the euphotic zone, upwelled DIC-rich deep water could release CO_2 and ultimately result in outgassing. On top of that, microbial respiration could be stimulated and accelerated by enhanced nutrients and subsequent phytoplankton labile DOC, and thus turn a productive upwelling area to be source rather than sink of CO_2. In terms of carbon sequestration, upwelling usually strengthen the POC-based BP. However, if picoplankton (e.g. *Prochlorococcus*) rather than net phytoplankton (e.g., diatoms) dominate the system, their non-sinking POC favor the microbial loop rather than the BP. Nevertheless, even if the BP is severely weaken, RDOC formation by the MCP can still work well, and carbon sequestration takes place while an upwelling area is outgassing. Given the tremendous complexity of the biological and biogeochemical responses to upwelling events, further high-frequency sampling and simultaneous observations of the BP and the MCP in the field is essential for a better understanding of carbon sequestration in the ocean.

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Table 1. Hydrographic characteristics, phytoplankton, particle export parameters, bacterial abundance and respiration and air–sea CO_2 flux in CE1, CE2 and surrounding waters. CE1: cyclonic eddy #1; CE2: cyclonic eddy #2. Error bars indicate standard deviation. TChl *a*: total chlorophyll *a*; SS: stable state; POC: particle organic carbon; BA: bacterial abundance; BR: bacterial respiration rate.

Parameters	CE1	CE2	Reference site
Hydrography			
Temperature (°C, at 25 m)	27.72[a]	23.33[b]	29.63[c]
Salinity (PSU, at 25 m)	34.12[a]	34.08[b]	33.99[c]
AOU (mol m^{-2}, 50–100 m)	4.83[a]	5.89[b]	2.31[c]
Phytoplankton[d]			
TChl *a* (mg m^{-2}, 0–50 m)	12.3 ± 3.68 (N = 23)	13.8 ± 4.91 (N = 11)	10.1 ± 7.89 (N = 47)
Fucoxanthin (mg m^{-2}, 0–50 m)	0.60 ± 0.26 (N = 23)	1.14 ± 1.10 (N = 11)	1.07 ± 1.89 (N = 47)
Divinyl chorophyll *a* (mg m^{-2}, 0–50 m)	2.88 ± 1.13 (N = 23)	1.97 ± 2.02 (N = 11)	1.72 ± 0.90 (N = 47)
Particle export[d]			
SS ^{234}Th flux @100 m (dpm m^{-2} d^{-1})	712 ± 521 (N = 8)	1609 ± 572 (N = 6)	1279 ± 697 (N = 10)
POC ($\times 10^2$ mol Cm^{-2}, 0–100 m)	1.76 ± 0.26 (N = 8)	2.18 ± 0.38 (N = 6)	1.78 ± 0.35 (N = 10)
POC/^{234}Th @100 m (μmol C dpm^{-1})	3.43 ± 1.00 (N = 8)	3.66 ± 1.00 (N = 6)	3.66 ± 1.12 (N = 10)
POC export @100 m (mmol C m^{-2} d^{-1})	2.50 ± 2.03 (N = 8)	6.16 ± 3.74 (N = 6)	4.92 ± 3.63 (N = 10)
Bacteria			
BA (10^5 cells mL^{-1})	2.41 ± 0.36 [d] (N = 2)	1.73[b]	2.14[c]
BR (mg Cm^{-2} d^{-1}, 0–100 m)	327 ± 28.2 [d] (N = 2)	255[b]	292[c]
Air-sea CO_2 flux[d]			
CO_2 flux (mmol m^{-2} d^{-1})	4.15 ± 0.84 (N = 9112)	3.43 ± 0.59 (N = 1330)	2.82 ± 0.65 (N = 13 754)

[a] Data from the CE1 center site TS1. [b] Data from the CE2 center site Y12. [c] Data from the reference site SEATS. [d] Data were mean ± SD (standard deviation) from the CE1 and CE2 regions and the reference sites of surrounding waters.

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Table 2. Bacterial respiration inside and outside the mesoscale features in the Atlantic.

Study area	Study site	BR[a] (mg C m^{-3} d^{-1}, 0–100 m)	Reference
Northeast Atlantic			
	Ambient Stn159	54.16	Lochte et al. (1987)
	Eddy centre Stn161	31.75	
	Eddy centre Stn162	32.04	
	Eddy margin Stn163	37.18	
	Ambient Stn164	16.23	
	Reference station Stn170	3.35	
Northwestern Sargasso Sea			
	Eddy 1 edge (N = 10)	2.05	Ewart et al. (2008)
	Eddy 1 center (N = 3)	1.68	
	Eddy 2 edge (N = 3)	2.31	
	Eddy 2 center (N = 1)	1.85	
BATS			
	Cyclonic eddies B178	7.39	
	Reference data[b]	3.08	
Sargasso Sea			
	Cyclones	0.20	Mourinõ-Carballido (2009)
BATS			
	Cyclones center	1.09	
	Cyclones edge	0.01	
	Anticyclone	0.64	
	CA[c]	−0.55	
The Canary Islands (15~19° W, 27~29° N)			
	Cyclone1	18.72	Baltar et al. (2010)
	Far-fields (FF)1	24.44	
	Cyclone2	12.63	
	Far-fields (FF)2	3.62	

[a] Bacterial respiration rate (BR) was calculated using BR = (BG × ICF × CCF) (1/BGE – 1) according to the bacterial production derived from the references.
[b] Reference data from the BATS summer climatology (1999–2002).
[c] Corresponds to areas of interaction between cyclone and anticyclone eddies.

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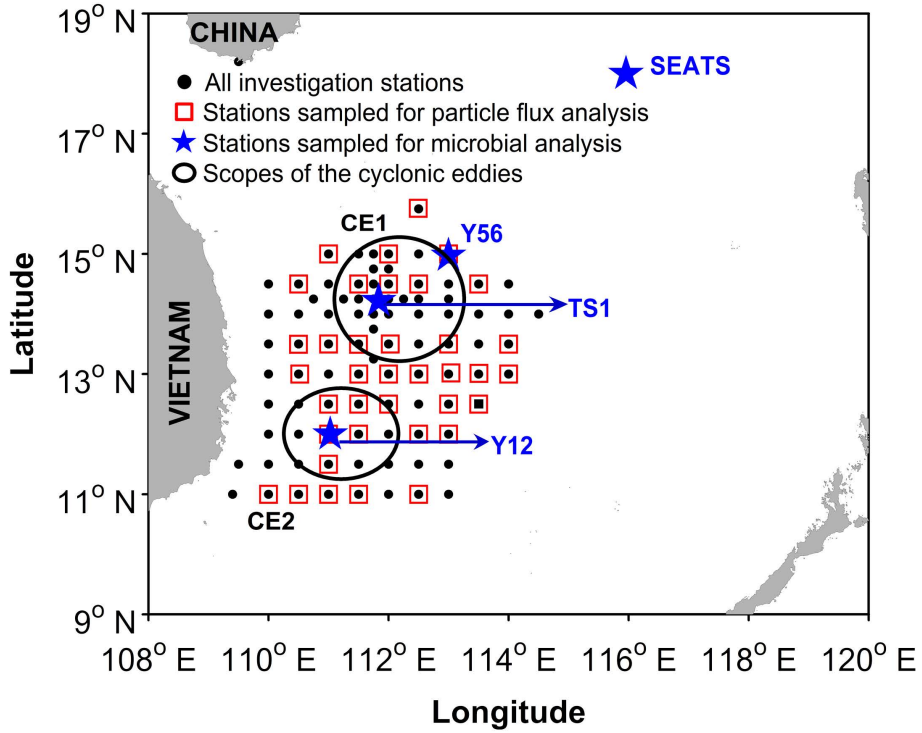

Fig. 1. Location of the study sites in the South China Sea. CE1: cold-core cyclonic eddy #1; CE2: cold-core cyclonic eddy #2. St. SEATS represents the South East Asia Time Series Station.

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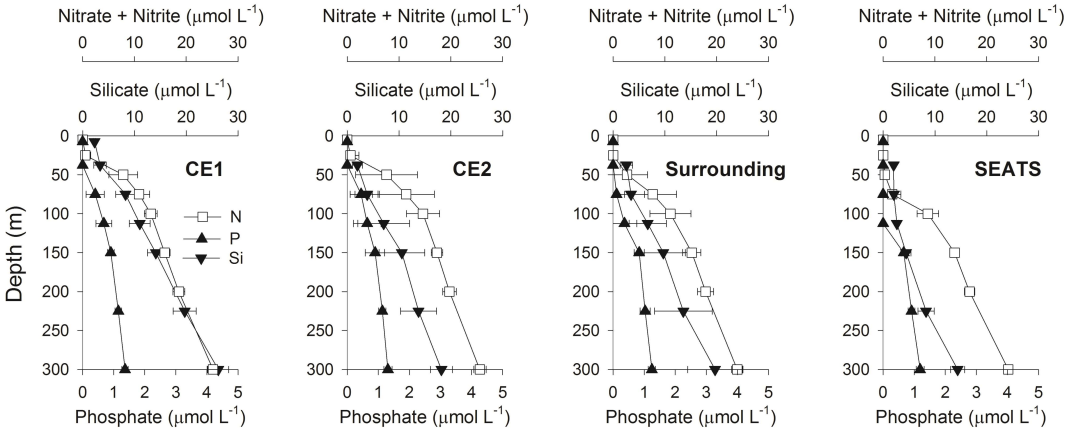

Fig. 2. Depth profiles of nutrient concentration averaged over respective stations inside and outside the eddies and the reference site (St. SEATS). Value "0" means below the detection limit of the standard spectrophotometric methods. Error bars indicate standard deviations.

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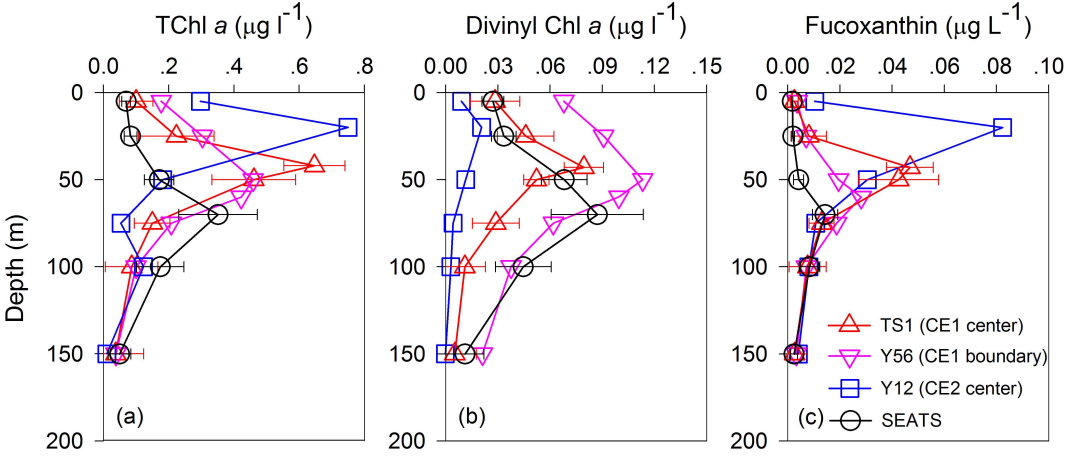

Fig. 3. Depth profiles of phytoplankton pigments at the eddy centers (TS1 and Y12), the eddy edge (Y56) and the reference site (St. SEATS). Data were the average values over time series analysis at St. TS1 and SEATS. Error bars indicate standard deviations. TChl *a*: total chlorophyll *a*.

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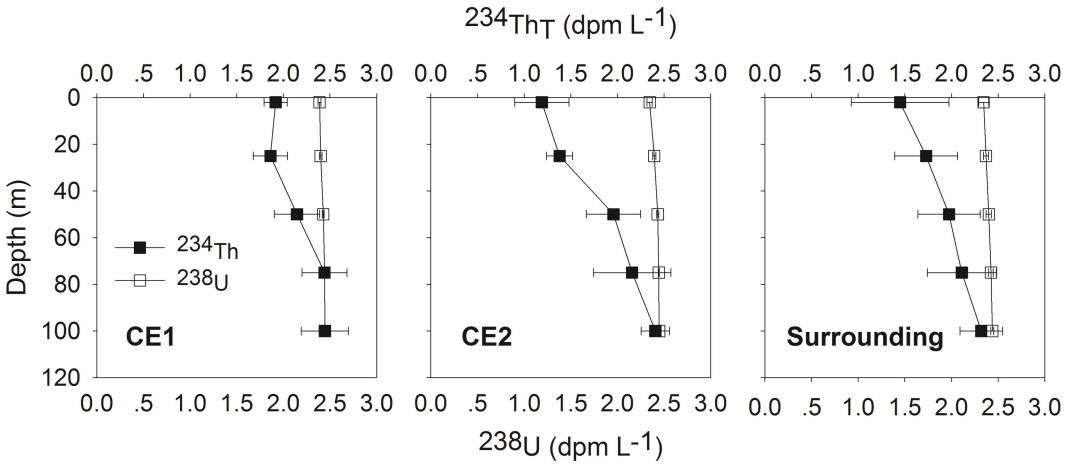

Fig. 4. Depth profiles of ^{234}Th and ^{238}U activities averaged over respective stations inside and outside the eddies. Error bars indicate standard deviations.

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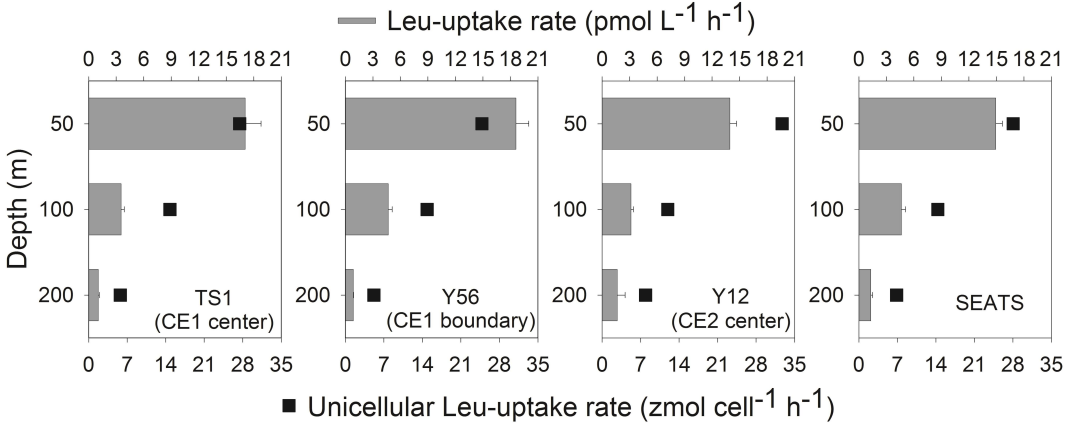

Fig. 5. Bulk leucine incorporation rates, abundance-specific (unicellular) leucine incorporation rates at representative depths in the eddy centers (TS1 and Y12), the eddy edge (Y56) and the reference site (St. SEATS).

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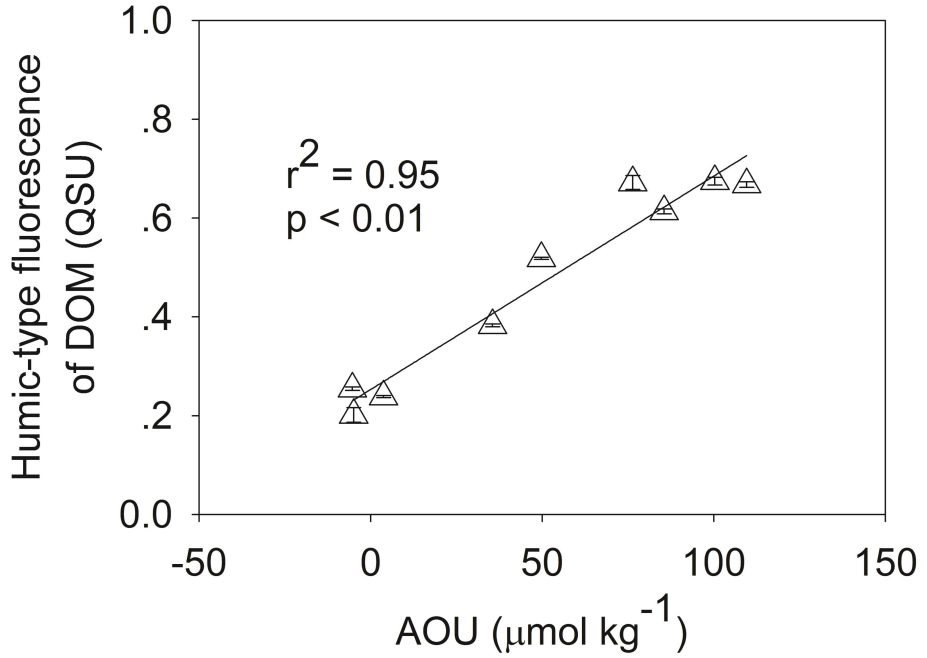

Fig. 6. Relationships between humic-type fluorescent dissolved organic matter (FDOM) and apparent oxygen utilization (AOU) in the euphotic zone of CE1. Error bars indicate standard deviations.

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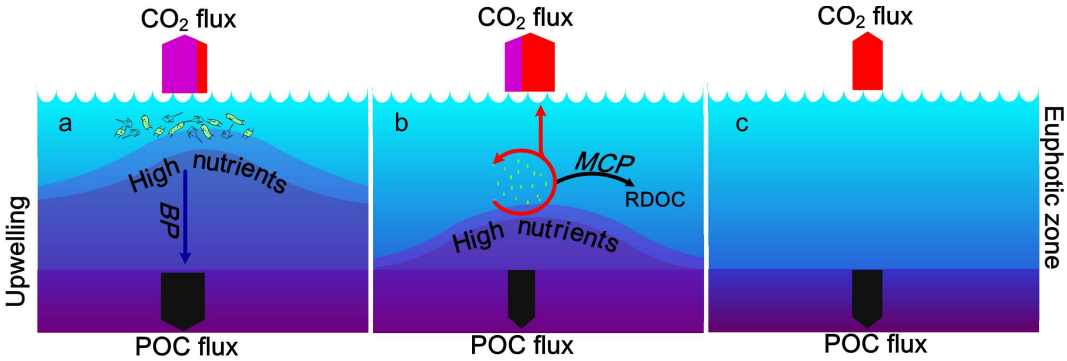

Fig. 7. Scenario models for a marine upwelling region to be a source or sink of CO_2. **(a)** Sink scenario: nutrients are injected into the upper layer of the euphotic zone; diatoms are dominant; POC export exceeds CO_2 outgassing; the biological pump is the prevailing mechanism for carbon sequestration. **(b)** Source scenario: nutrients are injected only into the lower layer of the euphotic zone; *Prochlorococcus* are dominant; microbial respiration is mobilized; CO_2 outgassing exceeds POC export; the MCP is the prevailing mechanism for carbon sequestration. **(c)** A non-upwelling scenario for reference.

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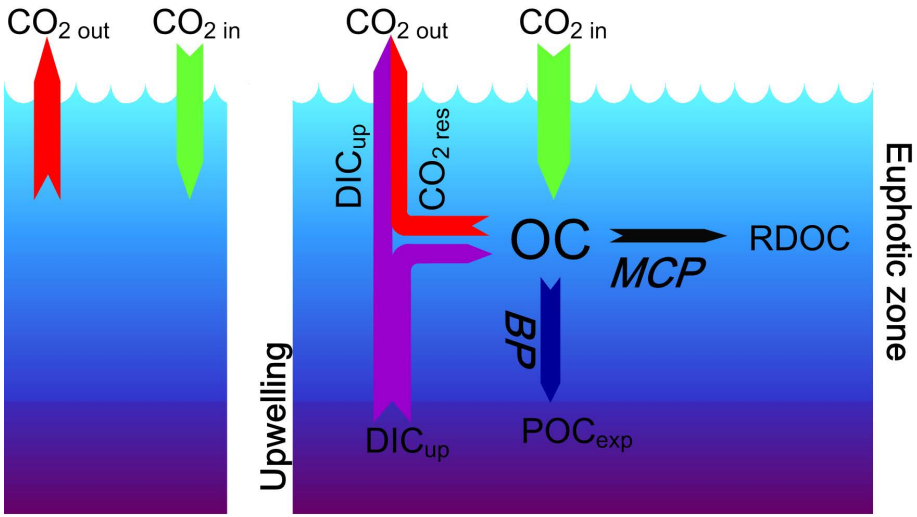

Fig. 8. A diagram showing the difference in carbon "sink"/"source" between non-upwelling area (left) and upwelling area (right). $CO_{2\ in}$: CO_2 dissolving into the sea from atmosphere; $CO_{2\ out}$: CO_2 released from the ocean; OC: organic carbon; RDOC: refractory dissolved organic carbon which could stay in the water column for long term storage; POC_{exp}: particulate organic carbon exported out of the euphotic zone; DIC_{up}: dissolved inorganic carbon in the upwelled water, which can be further released into the atmosphere when conditions permit; $CO_{2\ res}$: CO_2 from respiration. See the text for further details. Right panel also shows that carbon sequestration takes place through the BP and MCP in an upwelling area even if it is outgassing.

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